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THE ROLE OF WATERCRESS, *NASTURTIUM OFFICINALE*

AS A HOST OF NATIVE AND INTRODUCED PIERID BUTTERFLIES IN CALIFORNIA

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The mustard family, Cruciferae, has a very distinctive insect fauna. The chemical basis for host selection by Crucifer insects was demonstrated as early as 1911 by Verschaeffelt, and has more recently stimulated both physiological and ecological studies (e.g. Thorsteinson, 1953; Schoonhoven, 1967; Feeny, Paauwe, and Demong, 1970). Root and Tahvanainen (1969) pointed out that, because of their dependence on mustard oils as phagostimulants, multivoltine Crucifer insects may require a seasonal succession of host species in a given locality. Many Crucifers are short-lived annuals, and even many perennial species (such as members of the genus *Dentaria*) are seasonally ephemeral. In the northeastern United States wintercress, *Barbarea vulgaris* R. Br., forms a critical element in the seasonal succession because it is the only very common Crucifer which overwinters as a well-developed rosette; it is thus available to many insects when alternative hosts are not. In lowland California most Crucifers are vernal species which disappear during the long, hot, dry summer. On the floor of the Sacramento Valley the introduced multivoltine cabbage butterfly, *Pieris rapae* Linnaeus (Lepidoptera, Pieridae) and the harlequin stinkbug, *Murgantia histrionica* Hahn. (Hemiptera, Pentatomidae), are able to continue breeding through the summer on two introduced weedy, perennial Crucifers, *Lepidium latifolium* L. and *Brassica geniculata* (Desf.) J. Ball. (Shapiro, unpublished data). Over a wide elevational range in the Sierra Nevada introduced watercress, *Nasturtium officinale* R. Br. (= *Rorippa nasturtium-*

aquaticum Schinz. and Thell.) appears to have a distinctive ecological role as a host to both native and introduced Crucifer insects. This paper reports its impact on the seasonality and spatial distribution of two Pierid butterflies, *Pieris napi microstriata* J. A. Comstock and *P. rapae.*

BIOLOGY OF THE PLANT

Nasturtium officinale is a succulent, perennial aquatic weed, native to Europe. Unfortunately there appears to be no archeological evidence to date its introduction into California (Robbins, 1940). Major waves of weed introduction occurred in the Mission period (1769-1800) and the Gold Rush (1849-1860s). Watercress is widely naturalized in California, forming well-defined colonies in shaded, quiet, shallow, flowing water from near sea level (about 40 feet, Fair Oaks, Sacramento County) to at least 7000 feet (Nevada, Placer Counties) (fig. 1). The plant cannot tolerate prolonged desiccation and is thus mostly confined to permanent streams. It colonizes intermittent springs, seeps, or runoff channels, but behaves as an annual there and is generally stunted. In the lower part of its elevational range it may have two seasonal maxima of flowering, one in spring and another in late summer. At higher elevations the flowering period is in early- to midsummer. As the seeds ripen the tops die back and new growth begins from the base and sometimes from nodes on the creeping stems. The plant overwinters as rosettes, which commence rapid growth in late winter or very early spring. Unlike the native perennial Crucifer *Dentaria californica* Nutt. which often grows near it on the sides of canyons, *N. officinale* is green and available to insects for most of the warm season. In its lower elevational range in the foothills it is normally the *only* Crucifer which is green in summer.

HOST RELATIONS OF *PIERIS NAPI*

Pieris napi is a Holarctic species or species complex occurring naturally (not by human intervention) in most of the cooler and montane parts of Eurasia and North America. The subspecies *P. n. microstriata* is confined to riparian habitats, generally in canyons, on the east slope of the Coast Ranges and the west slope of the Sierra Nevada in California. It is characteristically spring-univoltine and monophenic, unlike the coastal fog-belt sub-

Fig. 1.—Habitat of watercress, *Nasturtium officinale,* in stream bed, Washington Creek, Nevada Co., California; male *Pieris napi* fly up and down the stream bed "patrolling" for newly-emerged females.

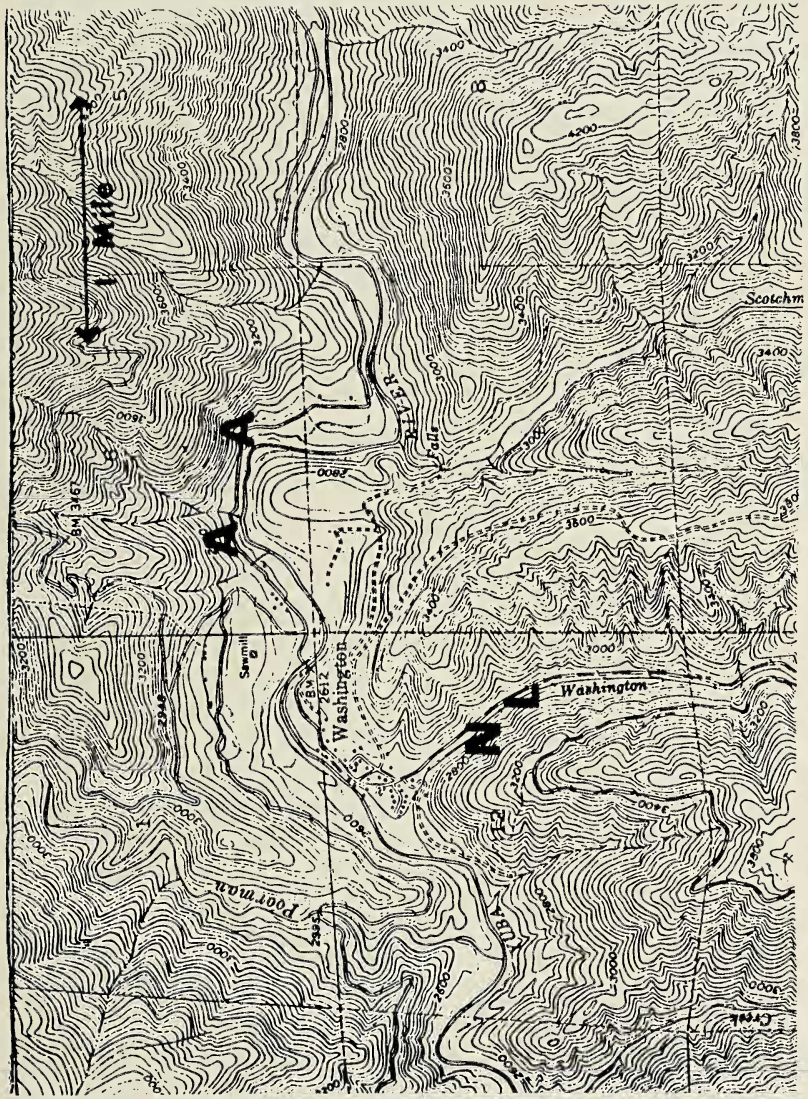

Fig. 2.—Spatial distribution of host records at Washington, Nevada County. A = *Arabis glabra;* N = *Nasturtium officinale;* L = *Lepidium virginicum* (see text).

species *venosa* Scudder (Shapiro, 1975a). In the literature its usual host association is *Dentaria californica,* whose vernal-ephemeral phenology generally fits that of the insect. Shapiro (1975b) reported *P. n. microstriata* breeding on *Arabis glabra* (L.) Bernh., a native annual, but not ovipositing on *Barbarea orthoceras* Ledeb., a native biennial, at Washington (2600 feet) and Lang Crossing (4500 feet) (both Nevada County); these are both spring plants. The development of local oviposition preferences seems to be routine for this animal. Thus at Baxter, Placer County (3900 feet) on 31 May 1975 three female *P. n. microstriata* were observed for about 20 minutes as they oviposited in a mixed stand of *Barbarea verna* (Mill.) Asch., *Lepidium campestre* (L.) R. Br., and *Arabis glabra*: eggs were laid only on the last. All three plant species were flowering and beginning to set fruit, and the females visited the blossoms of *B. verna* repeatedly. About 500 feet away many plants of *Lepidium virginicum* L. var. *pubescens* (Greene) Thell. (mostly not yet in flower) were growing in the road in much stronger sunshine, and they were not visited at all. (However, on 23 May 1975 several *P. napi* ova were found on this plant at Washington; see below.)

P. NAPI ON WATERCRESS

Given this selectivity, it is extremely striking that *P. n. microstriata* will apparently breed on *N. officinale* wherever the ranges of plant and insect coincide. The use of this plant was first called to my attention by R. L. Langston, who subsequently (1975) published it. Langston observed ovipositions on this plant near Placerville, El Dorado County (1850 feet). This locality was confirmed in 1975 and, more strikingly, *P. napi* was found breeding on watercress in close proximity to the localities where the host-selection observations reported in Shapiro, 1975b had been made. The spatial relationship between watercress and *Arabis* sites at Washington and Lang Crossing is shown in figures 2 and 3. Within the immediate vicinity of these sites the butterfly fails to utilize *Barbarea orthoceras* and *Lepidium campestre* although these plants are growing along *napi* "flyways" and may even be visited for nectar. *Lepidium virginicum* normally grows in quite different sites in full sun, but at Washington several plants were found in shade by the roadside a few feet from the stream bed where *P. napi* was breeding on watercress, and larvae were reared successfully to the adult from wild ova found on these plants.

At the altitude of Washington or Lang Crossing the phenology of *N. officinale* rather closely matches that of *Arabis glabra,*

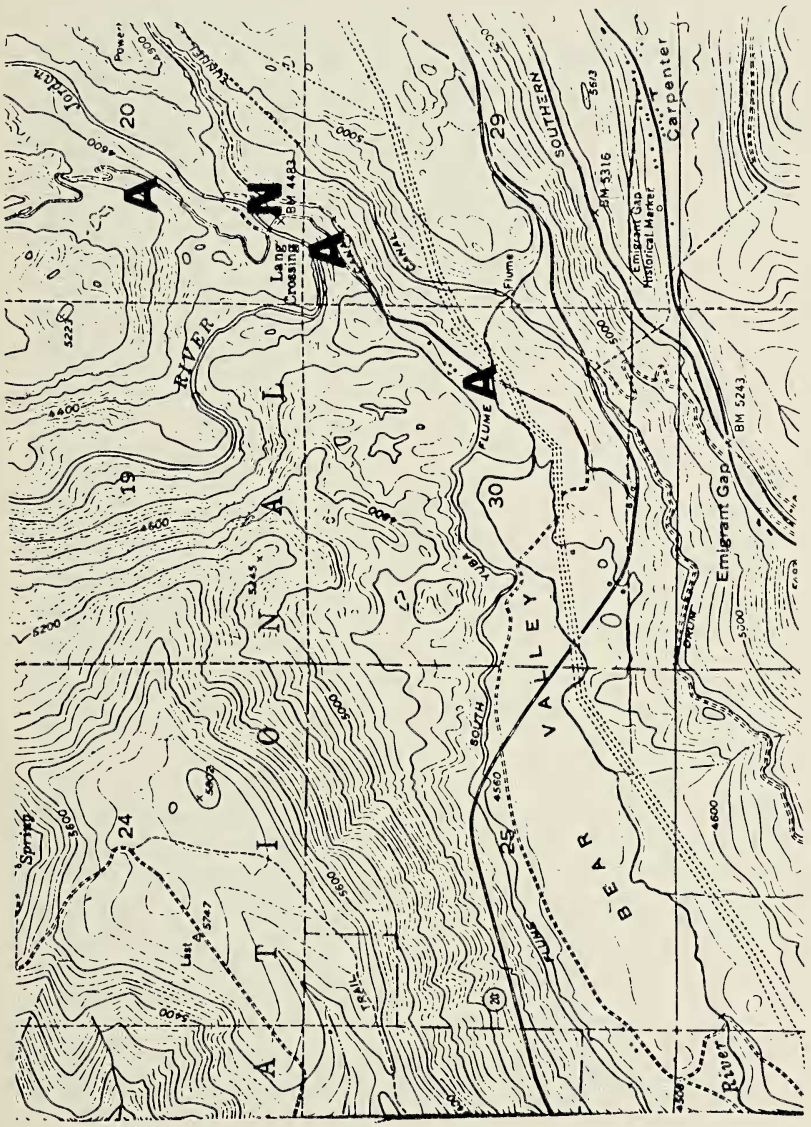

Fig. 3.—Spatial distribution of host records at Lang Crossing, Nevada County. Symbols as in figure 2 (see text).

and the seasonality of *P. napi* is unlikely to be altered by its presence. The butterfly is, however, undoubtedly able to maintain larger populations with than without it. Moreover, as it is perennial and occupies the same location from year to year, it provides a more reliable food source than does *A. glabra,* a successional species whose numbers may fluctuate widely from year to year. In this regard *N. officinale* resembles the native host *Dentaria.*

The situation is rather different in the foothills. Here the introduction of *N. officinale* may have allowed *P. napi* to expand both its range and its seasonality. The butterfly is common near Auburn in the American River gorge (Placer - El Dorado Counties, circa 650 feet) and is generally univoltine there as elsewhere in the Sierra Nevada, flying in early spring (March). In most of the gorge *N. officinale* is the *only* Crucifer. In two sites (fig. 4) *P. napi* is partially bivoltine in heavily shaded, cool, moist ravines where it breeds on lush growths of watercress. Although this bivoltinism appears to be due to microclimate rather than any genetic difference from adjacent univoltine populations (Shapiro, in preparation), neither uni- nor bivoltine *P. napi* could exist at all here in the absence of this introduced plant. Since California *P. napi* selects shaded ravine-riparian habitats, the preference of the plant for exactly these situations preadapted it as a host.

HOST RELATIONS OF *PIERIS RAPAE*

The European cabbage butterfly is generally considered to have entered North America in Quebec about 1860, but Reakirt's description of *Pieris yreka,* which appears to be this species, from California as 1867 suggests an earlier introduction there, possibly by the Spanish during the Mission period. *P. rapae* is now very widely distributed, from sea level to at least 8000 feet in disturbed habitats. It has a very long list of host records from lowland California (Shapiro, 1975c), but individual females tend to oviposit successively on the same Crucifer species, ignoring other potential hosts (unpublished notes). On the middle west slope of the Sierra its host preferences broadly overlap *P. napi,* including watercress and *Arabis glabra* but extending also to *Barbarea* and the two *Lepidiums.* Eggs and larvae of *P. rapae* have been collected from both watercress and *Arabis glabra* at both Washington and Lang Crossing, often from the

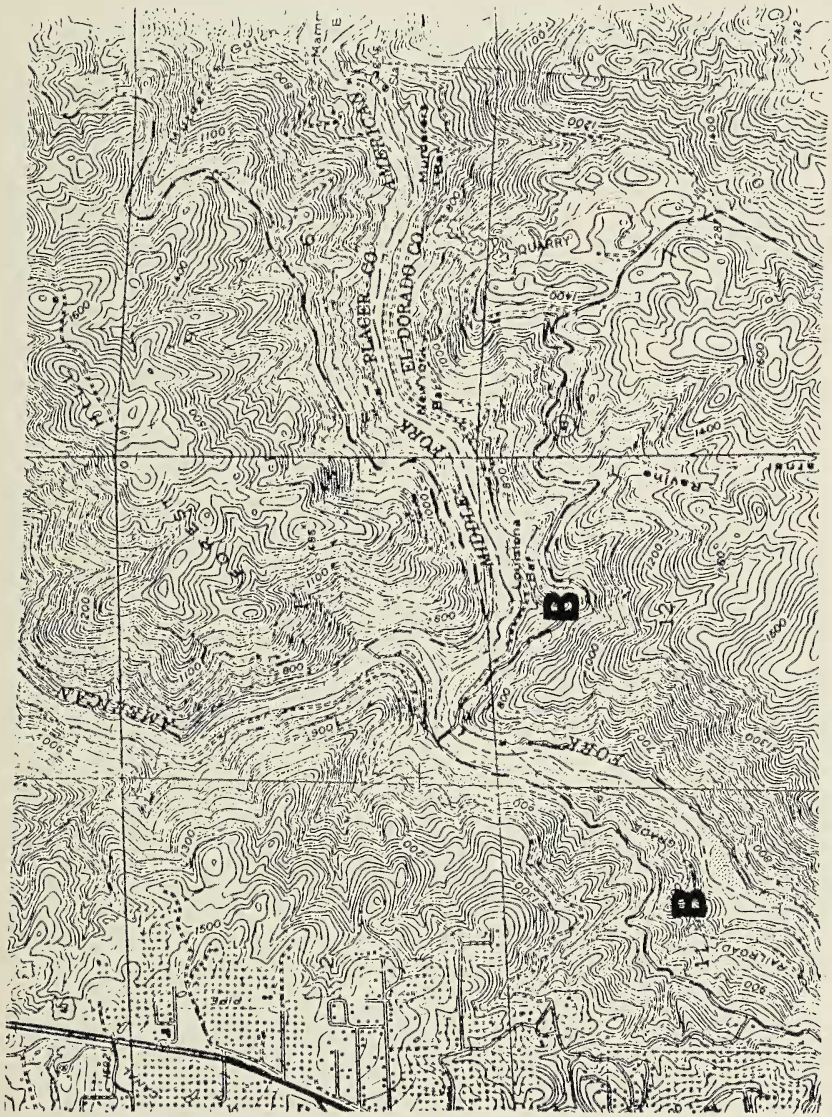

Fig. 4.—Locations of bivoltine *Nasturtium*-feeding populations of *Pieris napi* in the American River gorge near Auburn, California (see text).

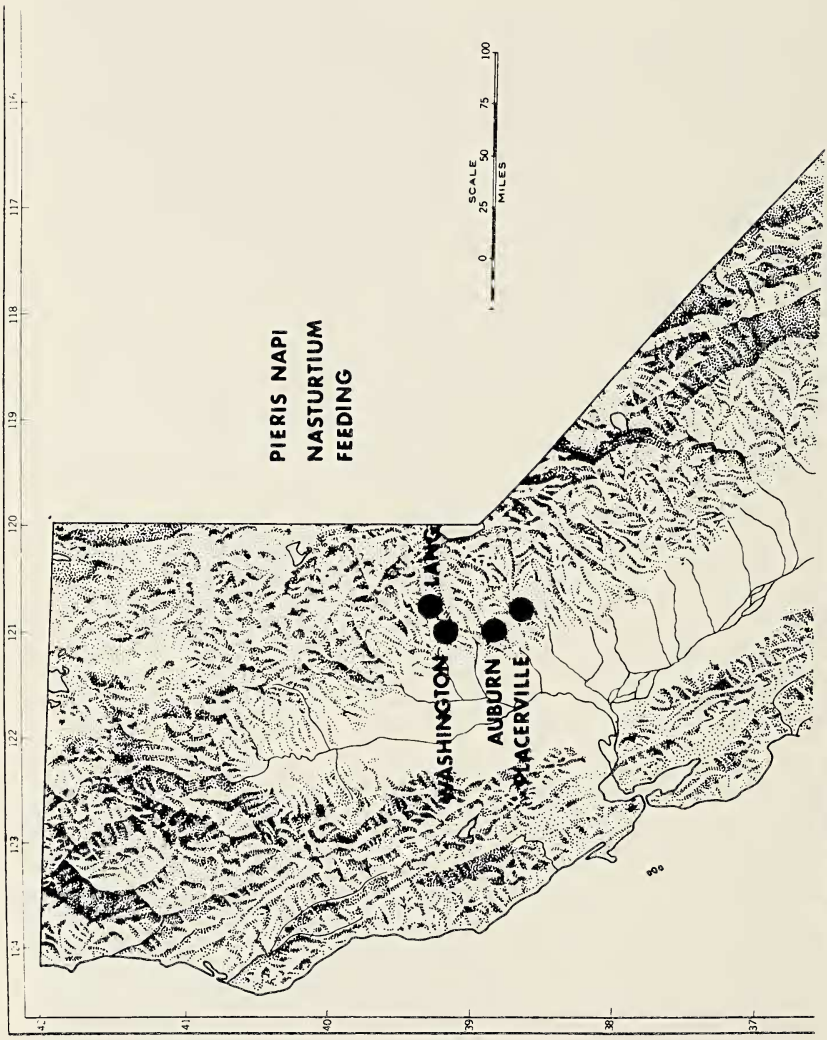

Fig. 5.—Localities where *P. napi* is known to feed on watercress in the Sierra Nevada. (Map from California Insect Survey, Univ. of Calif., Berkeley.)

same individual plants as eggs and larvae of *P. napi*. *Pieris rapae* is at least bivoltine at both stations.

In the American River gorge *P. rapae* (like *P. napi*) would be unable to exist in most sites in the absence of watercress. (It does breed along the arid roadside on scattered plants of *Brassica geniculata* growing in disturbed soil.) In one of the ravines where *P. napi* is bivoltine, an attempt was made on 1 July 1975 to collect second-generation *napi* larvae on watercress. Careful search of the entire stand produced only ten larvae of *P. rapae*, despite the fact that female *napi* had been flying there ten days earlier. Conditions at this site are much more mesic than on the roadside mustard in full sun, and wild *P. rapae* consistently prefers high water content Crucifers (such as *N. officinale*) over low water content species (*B. geniculata*) where a choice is available.

DISCUSSION

Lees and Archer (1974) group the hosts of *P. napi* in Britain according to field preference. They list watercress in group 1, i.e. plants on which females "were frequently and regularly observed to oviposit," and "from which larvae could readily be obtained by searching." There is no need to invoke genetic adaptation to a new host by Californian populations of *P. napi;* watercress seems to be intrinsically "desirable" as a *napi* host, and its utilization wherever it occurs on the Sierran west slope argues powerfully for this. It does have the potential disadvantage of liability to flash flooding, but this phenomenon was not actually observed at any Sierran locality under study in 1974 or 1975. Figure 5 summarizes the localities at which *P. napi* has been found breeding on watercress to date.

There is no native, aquatic, perennial Crucifer in the California flora. The native annual to biennial species *Rorippa curvisiliqua* (Hook.) Bessey has a wide elevational range, but grows in streams and seeps in meadow habitats, where Californian *P. napi* do not occur. (It is used by *P. rapae* at Donner Pass (7000 feet) (Shapiro, 1975d) but this butterfly has not been found on it in the Sacramento Valley. There, *R. curvisiliqua* is a spring species, very infrequent and inconspicuous compared to the rank, weedy "mustards.") The introduction of watercress, with its unique characteristics, permitted the expansion of the niches of the native butterfly *Pieris napi microstriata* and the introduced, weedy butterfly *P. rapae* in California. Its aquatic

perennial habit ideally preadapts it as a refuge for multivoltine species during the hot, dry lowland California summer and it may be expected to fill the same role for other members of the Crucifer fauna.

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